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A REVISION OF THE GENUS EPHUTA (MUTIL-LIDÆ) IN AMERICA NORTH OF MEXICO¹

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The genus *Ephuta* Say, together with the only other nearly related nearctic genus, *Timulla* Ashmead, includes some of the most polymorphic and difficult species complexes in the family Mutillidæ. The use of the term species in these two groups, often requires a great deal of courage and no end of imagination, since we have not yet arrived at the stage where quantitative study of large masses of material results in clear definition of what is a species, and what is a subspecies or merely individual variation.

The superficial uniformity of most of the species in both of these genera, both in vestiture and pigmentation, as well as in general body form, is coupled with a great deal of morphological variation in the males. To this must be added the baffling conservatism of the females, as regards evolution of specific characteristics that can be used to differentiate them. We thus are faced with a situation in which the considerable variation of the males leaves one in doubt where to draw the line between individual variation and geographic race, and between geographic race and species, while the superficial uniformity of the females prohibits their organization into definable taxonomic segregates

¹ Due to the length of this revision, it will appear in a number of separate sections, in this journal. The present part carries the paper through the keys to species. New binomials and trinomials will be properly validated by descriptions in succeeding parts of this work. The illustrations for the paper appear at the end of the present part; these also serve to illustrate subsequent portions of the work.

analogous to those evident in the male sex. In the only previous study of the nearctic species of the genus (Bradley, 1916) a single species was recognized in the female sex (though a second described species was unfortunately overlooked), and nine species were recognized in the male sex (while the tenth described species of male was also overlooked.) This very great difference in ratio between number of species known in the male sex, and number known in the female sex results from the interoperation of two factors: 1) the characters separating the female sex into species and races have not been adequately appreciated, 2) the females sometimes cannot be separated into morphological spe-Actually, a number of clearcut characters exist by which several species groups can be recognized in the female sex, while a number of additional characters are used tentatively here to separate several species and subspecies. There still exists a considerable discrepancy in the numbers of species and subspecies known in the male and female sex, though that numerical ratio has been considerably reduced by the present study. It is certain, however, that critical study of larger series of females than have been available to the author will result in more adequate diagnosis of some of the species than is now possible, and perhaps in further breaking up of the specific groups here recognized. It is felt, however, that with the present amount of date it would be scarcely justifiable to break up the female sex into a greater number of species, especially since the characters used for specific diagnosis are often so slight and subtle.

Some of the problems and lacunæ in the study of this genus that have either not been adequately treated, or which it has been impossible to touch upon with our present knowledge of the group are: (1) the relationships of the males and females; we have been able to correlate definitely the sexes of only one species with any certainty, (2) the exact range of many of the species and races, and the variation that is to be encountered from one end of the range of the form to the opposite end, (3) the amount of heterogonic growth involved, or where differences between individuals of different sizes is the result of some genetic, hence taxonomic, difference, (4) the lack of data on the ecology of the group, (5) inability to judge with certainty what is

heterogonic variation and what is geographical, or racial, variation.

The accumulation of data pointing toward a solution of all of these problems must certainly be regarded as forming the basis on which a sound taxonomic treatment of the group should be founded. Without at least some data of the above nature further, taxonomic study in the genus will be relatively sterile in results. The present treatment, in many ways merely an effort at pigeon-holing the various forms, can certainly be interpreted only as preparing the way for a more thorough study of the genus, based on some consideration of the above problems.

The species of nearctic *Ephuta* are perhaps less numerous in collections than those of any other moderate or large-sized Mutillid genus of the nearctic region. This relative scarcity has also been noted by Mickel for *Timulla* Ashmead. Both of these genera appear to be more fully represented in species and numbers in the neotropical region, though it must be stressed that the members of the Mutillinæ² are relatively poorly represented in the whole New World, compared with the Old World.

This scarcity of material in collections is the chief reason why problems two, three and five have been treated only in the case of the battlei-copano-sabaliana-spinifera-pauxilla complex of species and races. Of most of the species and lesser segregates we have seen less than a dozen individuals; of several of the forms only the holotype is known. This scarcity of material is chiefly responsible for the disposition as "species" of some segregates that possibly represent merely distinct races, or the separation as "subspecies" of forms that may indubitably be good species. It has been felt desirable to limit the term species to such forms as could be demonstrated in the present study to represent discrete entities differing in several major morphologigal characteristics from all of the closely related forms. In the female sex, unfortunately, major morphological differences scarcely exist, and some of the species there are to be interpreted as tentative only. The systematist in working on this genus is faced with the choice

² Used here in the restricted sense (See Schuster, 1946, 1949) for those genera with large, conchiform tegulæ, reniform facetted eyes with a sharp inner emargination, and with the stigmatic cell poorly developed or absent, and not uniformly sclerotized and pigmented.

of calling the more or less discrete morphological segregates of the several "Artenkreise" of males species, and to leaving the plethora as inseparable on non-morphological characters, or calling the males involved a single polymorphic species, consisting of many races (some of which would have to exist side by side, yet inexplicably remain distinct from each other), while the female is presumed to be uniform and not capable of separation into analogous subspecies. This latter solution, in some ways, is the easy way out of the difficulty. Yet it leaves one in the position of having to explain the occurrence together of three or four of these "subspecies" of males in the same locality. For instance, forms of battlei, pauxilla, and spinifera, occur side by side, in northern Virginia (and are represented in the type series of pauxilla Bradley), together with the certainly distinct E. scrupea. Yet the females of these four distinct species of males have not been previously separated and have been simply called "puteola" Blake. Employing characters the author does not regard as above suspicion, he has been able to separate the females of scrupea, pauxilla and spinifera from each other. At the same time, the occurrence of these discrete forms of males in the same locality indicates that they in all probability are not subspecies of each other, and that their individuals must be able to tell the difference between the females of the three forms involved. Therefore, the author prefers to believe that the first of the above alternatives proposed is the more probable one, and has been guided by that precept in the present study. (Since this was written a certain amount of corroboratory data have accumulated in favor of such a viewpoint).

Although, before this study, only a single female was recognized for the United States (Bradley, 1916), the author has been able to increase this to sixteen species, and four additional varieties or subspecies. Using various standard techniques, he has been able to correlate six of these females to species of males, and able to suggest several more probable correlations. One species (E. margueritæ) was correlated on the basis of material of both sexes bred from the same group of cocoons of the same host, hence probable progeny of a single female. A second species (E. argenticeps) was correlated on the basis of exclusion of

all other males and females, since the male and female assigned to it are the only ones known to occur in California. A third species (E. spinifera) was correlated on the basis of a male and female taken in copula by Mr. D. Shappirio, while several more males and females were taken at the same locality and time. Two other species ("puteola" portion and scrupea) were associated with their males on the basis of coincident distribution, and collections of the respective males and females at the same time and place, as well as differences in total range of the respective males and respective females. The sixth species (E. conchate) was associated with a female because of a suggestively similar east-west distribution in the Transition Zone of the eastern half of the United States, not matched by any other known male or female.

Study of mass collections made by Mr. D. Shappirio around Washington D. C. also made possible more clear-cut separation of the females of the *puteola-spinifera-scrupea* group. The long series made possible the analysis of the variation in each species of female, and the formation of some idea as to what represented merely vicarious modification within each species, and what represented valid taxonomic characters for species separation.³

Finally, it must be stressed that much more detailed study of larger series, with the ocular micrometer, must be undertaken,

³ It must be stressed that reduction of the females has been so extreme that recourse must be had to characteristics of extreme subtlety (such as slight differences in puncturation), that possess an inherent amplitude of variation within the species (especially correlated with size differences) often much greater than the gap between two species. The utilization of such characters is therefore extremely unsatisfactory. Therefore, study of long series from a restricted area and comparison of these individuals with those of other populations are alone able to provide an answer as to whether such minor characters are valid taxonomic characters, or merely part of the inherent variability of a more broadly conceived species.

Since the hundred-odd females sent for study by Mr. Shappirio all could be placed definitely by means of the included key, it was concluded that the separating characters had the necessary validity, however great their nicety. This material therefore served as a welcome test of the specific concepts arrived at on the basis of isolated individuals. Whether the species can be separated readily without comparative material, remains another question, since the differences are scarcely subject to exact definition in a key (although enough to lend a distinctive facies to the species).

and some effort made to critically define the limits of variation of the species and races. It is evident that there is in the males a great deal of variation in the degree of development of the ocelli and eyes, of the humeral prothoracic angles, of the transverse propodeal ridge, of the sculpture of the thorax and of the tegulæ, and in the type and degree of pigmentation of the hypopygium, as well as in the amount and type of vestiture. Large ocelli, strongly developed humeral angles, coarse sculpture, dense sericeous vestiture, are all derivative characters usually developed to their greatest degree in large individuals of any one species, and to a lesser degree in abnormally small individuals.4 When very small series, or only isolated, extreme individuals are at hand, interpretation of such possibly largely heterogonic variation as genetic variation may occur. Mickel (1924) has shown that differences on a nutritional level can result in a bimodal curve, as regards variation in size. If there is a corresponding distribution of degree of development of the specific characters, interpretation of each of the two main size groups as a distinct species may occur. Cautious interpretation of data derived from size of ocelli, and the spatial arrangement of the ocelli, of the relative widths of head and thorax, of the degree of development of the humeri, of the relative coarseness of the sculpture and density of vestiture is therefore a primary requisite of sound systematic work in this genus. It is quite possible, therefore, that abnormally small, and "underdeveloped" individuals of a specialized species could be confused with large, normally developed individuals of a less derivative species. This, in no way invalidates the two species as discrete entities, since all kinds of intergradation must occur between the large and small individuals of the one species, while there must exist some gap, however small, between the extreme individuals of the two species, that is not bridged by annectant forms. The distinction between species and subspecies in the following keys are drawn from normal, well-developed individuals. Therefore, when the statement "humeri strongly produced" is made, allowance must be made for the fact that abnormally small individuals may have them relatively weakly developed. Some knowledge of the variation in size of the species is thus necessary.

⁴ See tables at the end of this revision.

In this preliminary monograph of the nearctic members of the genus thirty-two new species and subspecies and varieties have been described. This, together with the ten species treated by Bradley (1916), together with E. rufisquamis André, and E. sudatrix Melander (which were omitted by Bradley), and E. conchate Mickel (described subsequently), while subtracting E. susura (Melander) which is subsequently synonymized, results in forty-four nearctic forms. There are probably at least four times as many species of this entirely New World genus in the neotropical region. The species from Mexico, Central America, and the West Indies, which connect our forms with the more strictly tropical species, have been recently treated by the writer (Schuster, 1945). Study of the much more highly specialized tropical forms indicates the genus is conceivably a relatively recent invasion of the nearctic region, with the less specialized species being "forced" northward, to the periphery of distribution of the genus much as propounded by Matthews for the distribution of vertebrates.

This study was first initiated at Cornell University under the direction of Dr. J. C. Bradley, to whom the author would like to express sincerest appreciation for his aid. Study of a considerable body of material, subsequently, while at the University of Minnesota, resulted in revision of most of the manuscript. For the final revision, the writer would like to acknowledge the help and criticism of Drs. C. E. Mickel and A. Glenn Richards. He would also like to extend his thanks to Dr. Gunvantlal A. Patel, who helped in checking the key, to Dr. William T. M. Forbes, who critically examined the statistical data accumulated in the PAUXILLA complex. Finally, the author would like to express his appreciation for all the help given in the preparation of this manuscript by his wife, Olga M. Schuster. The encouragement received from Mr. and Mrs. Noah A. Bower and Mr. Harvey I. Scudder, at the outset of this study of the nearctic Mutillidæ has helped much in bringing forth this revision.

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Herbert F. Schwarz, of the American Museum of Natural History; Dr. C. S. Brimley of the North Carolina Department of Agriculture; Dr. Henry Dietrich, of Cornell University, Messrs. Chapin, Townes and Krombein of the United States National Museum; Dr. A. C. Cole, Jr. of the University of Tennessee; Mr. David G. Shappirio.

Genus Ephuta Say

Mutilla, auctorum.

Ephuta Say (partim) Boston Journ. Nat. Hist., 1, p. 297, 1836.

Mutilla subgenus Mutilla (Divisions II and III) Blake, Trans.

Amer. Ent. Soc., 3, pp. 230, 232, 1871.

Mutilla, subgenus Sphæropthalma (Division I, subdivision II, in part) Blake, idem, pp. 232, 246.

Ephuta Ashmead, Jour. N. Y. Ent. Soc., 7: p. 57, 1899.

Ronisia Ashmead (not Costa), idem. p. 58. (acc. André).

Mutilla, group scrupea Fox, Trans. Amer. Ent. Soc., 25, p. 272, 1899.

Rhoptromutilla André, Gen. Insectorum, fasc. 11, p. 43, 1903. Ephutopsis Ashmead, Can. Ent., 36, p. 6, 1904.

Ephuta Bradley, Trans. Amer. Ent. Soc., 42, p. 192, 1916.

Ephuta Mickel, 19th Rep. State Ent. Minn., p. 111, 1923.

Ephuta Schuster, Rev. Ent. (Rio), 16, pp. 187-204, 1945.

Ephuta Schuster, Annals Ent. Soc. Amer., 39, p. 703, 1946.

Genotype:—Ephuta scrupea Say (Ashmead, Journ. N. Y. Ent. Soc., 7, p. 57, 1899). Say in 1836 described the genus Ephuta as a subgeneric segregate from Mutilla L. and included three species in it, erythrina, gibbosa and scrupea. His description applies only to the first two, since it reads "Eyes entire or emargination obsolete." Ashmead, no doubt through some oversight, selected the last species as the genotype thus giving the genus an entirely different meaning from that intended by Say. André (1903) did not accept Ashmead's unfortunate type designation and described Rhoptromutilla, with M. chrysodora Perty as type, to include what we now call Ephuta. André used Ephuta in the sense indicated by Say's diagnosis, and his Ephuta therefore is largely synonomous with Dasymutilla Ashmead. Ashmead's type designation was valid under the International Rules of Nomenclature and *Ephuta* therefore stands as limited by him.

Ashmead (1904) made *Ephuta* the type genus of his tribe *Ephutini*. This latter group was an artificial pigeon-hole that has not found any acceptance. In 1945, the writer re-evaluated the characters of the group and came to the conclusion that *Ephutopsis* Ashmead, the only other generic segregate that could clearly be included in the *Ephutini*, was not generically distinct from *Ephuta*. In 1946, the writer rescued the name *Ephutini* from oblivion, and diagnosed it briefly, placing it as a tribe of Mutillinæ, with the genus *Ephuta* as type genus. The latter is the only included genus. This use of the tribal name *Ephutini* is not at all equivalent to the sense in which it was employed by Ashmead. The tribe as emended includes only the neogeic forms of the genus *Ephuta*, and the tribal characters may be briefly stated as follows:

Tribe EPHUTINI Ashmead (1904), emend. Schuster (1946)

MALES.—Tegulæ large, conchiform; (Fig. 37) eyes reniform, facetted distinctly, deeply emarginate within (Fig. 37); mandibles normally 2-dentate distally, ventrally devoid of all trace of teeth, or of emargination (Fig. 10, 24); mesopleura lacking the oblique sulcus (Fig. 37), evenly convex (except in a few, relatively generalized, neotropical species); propodeum areolate, frequently variously armed. Wings lacking a stigma; cells R₄ and M₂ indicated by color lines or delicate veins (Fig. 1). Abdomen with petiole extremely narrow, subterete, cylindrical, usually equally or subequally wide basally and distally (Fig. 37), very short and transverse to elongate; second segment lacking felt lines; tergites 5-7 (and usually 3-4) with a longitudinal median carina; second and distal sternites devoid of all trace of lateral or median processes, tubercles, or carinæ.

FEMALES.—Eyes ovate, silvery, strongly facetted (Figs. 38, 39); supraclypeal ridge quadridentate normally (Figs. 38, 39); mandibles entire below, falcate, slender (Figs. 38-41); hypostomal ridge running back from mandibular posterior condyle angulate or dentiform produced (Figs. 40-41); alitrunk highly reduced, elliptical or ovate, with pleura punctate throughout and rounded gradually into notum (Fig. 25); lateral sutures entirely lost on pleuræ, including the pronotal-mesopleural suture. Gaster with petiole as in male, (Fig. 25); second segment with felt lines absent or represented by foveate pits or grooves; distal tergites not carinate as in male (Fig. 25); pygidium undefined or delicately delimited distally by faint carinæ, usually polished and very small (Figs. 25-26, 31, 34, 35); hypopgium usually with a pair of basal, lateral tubercles, often connected by a transverse ridge (Figs. 27-30, 32-33, 36).

The Tribe *Ephutini* may be contrasted to the *Mutillini* (in which, tentatively at least, the writer would include all the other genera of Mutillinæ), as follows:

Both sexes with petiole gradually dilated, broad, evenly and fully continuous and sessile with second tergite; felt lines present on second tergite (and often second sternite), except in Areotilla Bisch. Male with abdominal distal tergites not longitudinally carinate medially; mandibles usually with at least a trace of ventral excision and a ventral tooth; wings with a small to distinct stigmatic cell usually retained (distance between origin of M. on R+M and apex of stigma usually varying from 0.7–1.2 the length of marginal cell on costa); origin of $r-m+R_s$ on M midway between origin of m-cu and M_{3+4} , or nearer M_{3+4} . Female with alitrunk with the pleura at a distinct angle to the notum, largely or entirely devoid of coarser sculpture, generally with retention of traces of sutures, the dorsal outline varying generally from rectangular to hour-glass shaped: never strongly narrowed both anteriorly and posteriorly. TRIBE MUTILLINI.

Both sexes with petiole nearly or quite parallel-sided, narrow, not dilated distally, sharply separated dorsally from the second tergite; felt lines absent on both tergite and sternite (at most analogous pit- or groove-like structures on the second tergite of the $\mathfrak P$). Male with distal abdominal tergites longitudinally carinate; mandibles entire below; wings with stigmatic cell obsolete (Fig. 1) (distance between origin of M on R+M and apex of stigma 0.3–0.5 the length of marginal cell on costa); origin of r-m +R_s much nearer origin of m-cu than of M₃₊₄. Female with alitrunk with pleura evenly continuous with notum, sculptured like notum and totally devoid of all traces of sutures, the dorsal outline narrowly ovoid of elliptical. TRIBE EPHUTINI

DIAGNOSTIC CHARACTERS OF GENUS

Males.—Eyes large, reniform-ovate, deeply and sharply excised on the upper portions of the inner orbits, very distinctly facetted (Figs. 10, 11, 24, 37). Antennæ short, robust, with the second flagellar segment transverse, wider than long (Fig. 37), little longer than the first (rarely elongate); the pedicel short, sub-globular; the scape bicarinate, the carinæ meeting in a loop distally (occasionally with one of the carinæ obsolete, and the enclosed face little defined) (Figs. 10-11). Clypeal area usually defined by a pair of prominent, more or less diverging subantennal carinæ (Figs. 2-10), that are usually dentiform produced at a variable distance down towards the anterior clypeal margin (Fig. 3d), and which may have the carinæ dorsad of that angulation fused into a single median carina; the clypeal basin (Fig. 2b) (and the subantennal (Fig. 2a), when not obliterated) entirely or virtually devoid of setigerous punctures, more or less polished. Antennal scrobes with a distinct, transversely oblique, truncate tooth dorsally (Figs. 10-11); antennal tubercules approximate, more or less sculptured. Mandibles bidentate (Figs. 10, 24), occasionally with a larger, third, dorsal, molar tooth developed (Fig. 11) usually falcate and always simple, unexcised ventrally. Clypeus rounded anteriorly, not bidentate (Fig. 2c).

Thorax with pronotum short medially, the humeri often more or less produced and carinate (Fig. 37); mesonotum with parapsidal furrows totally absent, occasionally weakly indicated (in some neotropical forms doubtfully indicated by broad, polished gutters); mesopleura evenly swollen, lacking the oblique sulcus and pit, (Fig. 37), occasionally (neotropical forms) spinose-produced above; mesosternum (in nearctic forms) never produced as gibbosities, carinæ, or teeth; scutellum flatly swollen to gibbous (Fig. 37), occasionally (in neotropical forms) carinate medially or sulcate medially, and with the posterior angles dentiform produced. Tegulæ large, strongly convex, conchiform with the posterior margin not reflexed, hiding the auxillary wing sclerites beneath them (Fig. 37). Propodeum often variously armed medially or laterally, often with a transverse ridge, always coarsely reticulate-areolate (Fig. 37), and with a median basal areole or areoles. Legs with small, unproduced trochanters; posterior coxe normal or armed; calcaria 1-2-2. Wings with stigma absent, cells R4 and 1st M2 more or less distinct, indicated at least by color lines; hind wings with basal part of Sc+R+M heavily sclerotized, the distal half or more, much less so; cell R₅ very elongate (Fig. 1).

Abdomen with petiole always very slender (Fig. 37), its width usually less than one-third that of second tergite, nearly parallel-sided in dorsal profile, with the form varying from short and transverse (all nearctic forms) to elongate and slender (many neotropical forms), in section subterete, with a low, sometimes anteriorly produced sternal carina (Fig. 37). Second segment with felt lines of the sternite always lacking, and absent on the tergite as well. Tergites 5-7 (and usually 3 and 4 as well) with a distinct median, delicate, longitudinal carinule. Vestiture of simple hairs throughout, lacking all types of specialized setæ or plumose hairs. Sternite two, and all distal sternites simple, lacking lateral carinæ or teeth; hypopygium simple, unarmed. Genitalia with the parameres ventrally decurved.

FEMALES.—Eyes large, ovate, entire, facetted, usually silvery (Figs. 38, 39); head transversely oval, with the eyes scarcely protruding (Fig. 25). Supraclypeal ridge or flange with several (usually four) distinct coarse teeth (Figs. 38-39); mandibles slender, distally bidentate, ventrally unarmed (Figs. 38-41). Antennal scrobes unarmed, lacking dorsal carinæ (Figs. 38, 39).

Alitrunk elliptical or oval, elongate, not more contracted anteriorly than posteriorly (Fig. 25), with the dorsum evenly, uniformly, closely punctured, the dorsum gradually rounded into the evenly convex pleura that are also evenly continuous with the posterior propodeal face, only the two pairs of spiracles protruding; all dorsal and lateral sutures lacking and the alitrunk much more highly reduced and simplified than in *Timulla* (and lacking trace of metanotal ("scutellar") scales and ridges) as well as the suture separating the lateral pronotal faces from the mesopleura.

Gaster with petiole similar to that of male, short and transverse, parallel-

sided (Fig. 25). Second segment, as in male, without felt lines (or, in some neotropical species, with modified grooves or pit-like ones of the second tergite); disk of tergite usually with two rounded or oval spots of silvery vestiture (often reduced or absent) and usually a distal band of similar hairs, more or less notched or emarginate in the middle) (Fig. 25). Distal segments not carinate as in male. Hypopygium more or less armed with a pair of basal lateral tubercles, often connected by a slight ridge (Figs. 27-30, 32, 36); distally the hypopygium may be entire (Figs. 27, 32-33) or weakly quadrilobed (Figs. 28-30). Pygidium with a distal, small, faintly defined area (Figs. 26, 31, 35), or virtually no area at all (Figs. 25, 34), the lateral carinules delicate, or virtually absent; the more or less defined small pygidial area is more or less convex, and usually polished (Fig. 26), at most slightly granulose or obscurely punctate-granulose (Fig. 31).

The males generally are black pigmented throughout, but may have the gaster iridescent and violaceous, or may have it more or less ferruginous. Rarely the ferruginous pigmentation extends over the whole body. The females are usually entirely ferruginous (occasionally, in tropical forms, with the head, or thorax, or head and abdomen more or less black). Both sexes have a more or less distinct band of silvery, dense, sericeous vestiture at the apex of the petiole, and a similar band at the apex of tergite two (Fig. 25) (except a few neotropical forms).

RELATIONSHIPS

The genus Ephuta is one of the most sharply and distinctly isolated of the genera of Mutillidæ. The form of the tegulæ, lack of a sclerotized stigmatic cell, the generally strongly decurved distal segments of the gaster, the nature of the eyes, and the distally decurved (rather than upcurved) parameres place it as a member of the Mutillinæ. It differs at once from all other genera of that subfamily in that the petiole is slender (Figs. 25, 37), and exhibits a constriction between it and the second tergite. In the linear or parallel-sided form of the petiole the genus, indeed, differs at once from all other Mutillid genera. The modification or loss of the felt lines also separates it at once from all other Mutillidæ, except those of the unrelated genus Rhopalo-The ventrally uniformly simple mandibles, of both mutilla. sexes, and the areolate propodeum of the male, as well as presence of median carinæ of the distal tergites of the males are other characters not generally found in other genera of Mutilline. In the female sex, the petiole form, as well as the highly modified and simplified form (Fig. 25) of the alitrunk (which is contracted evenly in front and back, and lacks all the primitive features of the pleura found in other genera), and the raised, transverse, more or less quadridentate supraclypeal ridge or arch (Figs. 38–39) are quite characteristic. The total loss in the female of the sutures separating the lateral pronotal faces from the mesopleura (below the prothoracic spiracular openings) separates the genus from almost all other Mutillid genera of which I have had available material in the female sex. The lack of felt lines is another highly important differentiating character, as well as the relatively poorly developed pygidium of the female which is polished or only very obscurely sculptured. The form of the hypopygium (always simple in the males; generally bituberculate at base in the female) is also diagnostic, as is the form of the clypeal region, and its configuration, in the male sex.

ECOLOGY

The ecology of the genus is virtually uninvestigated. We know very little regarding any phase of the biology of the genus, and nothing has been heretofore published. Certain observations, based both on field experience and study of the males, indicate that the various species do not prefer sandy regions, as do most of our other Mutillidæ. The absence of, or poorly developed pygidium of the females indicates that they are not adapted for digging; the lack of development of a comb of the anterior tarsi is further circumstantial proof that the various species are not fossorial.

The writer has observed the females at several times in the field, and finds that they occur most generally in areas overgrown by grasses and sedges, in which the bees of the genus Halictus and similar bees nest. A single female, of E. puteola, was observed in June, 1941, in Putnam County, New York, crawling among the clipped grass at the edge of a path, where Pseudomethoca frigida (Smith) and Myrmosa occurred. The species here appeared to be parasitic upon Halictus, among the tunnels of which it was found. A female observed in June 1946 on a small, low-lying island in Beebe Lake, Ithaca, New York, also occurred in open grassy land, crawling on moist, alluvial, pebbly soil. No possible hosts were observed here.

C. N. Ainslie has taken a series of males on the flowers of

Solidago, at Beach, North Dakota. These males, of Ephuta grisea Bradley, apparently were feeding on pollen. Harvey I. Scudder has taken the male E. conchate Mickel at Breesport, New York, feeding on the honey-dew of Myzus ribis, occurring on currant. Mr. Nathan Banks has also taken Ephuta (of the species pauxilla, scrupea, and spinifera), on the honey-dew of aphids on Liriodendron, the tulip tree. Although several species of the related genus Timulla have been reared from various hosts (Tiphia, Eumenes, and Odynerus, as well as the Dynastine beetle, Ligyrus gibbosus), there exist no previous records of any hosts of the genus Ephuta.

A male of *Ephuta scrupea* Say, from Enola, Pennsylvania has been examined bearing the following data: "Reared from cocoons of *Pseudagenia bombycina*" (collected by Kirk and Champlain). Three males and a single female of *E. margueritæ xanthocephala* sp. et subsp. n. have also been examined that were bred from "Hymenoptera —cocoons under stones — Rockville, Dauphin County, Pennsylvania." These had been collected May 1, 1910, by H. B. Kirk, and emerged May 23, 1910.

Another clue to a possible host species is given by a male of *Ephuta pauxilla*, collected by P. W. Fattig, which was taken with *Tiphia transversa*.

No other data on the ecology and biology of the genus is available at this time.⁶

DISTRIBUTION

The genus *Ephuta* is entirely New World in distribution. It is developed to its greatest degree in the tropical regions of Central and South America. The known distribution, as well as absence of a tarsal comb and a large, sculptured pygidial area of the female, indicates the genus is quite or nearly absent from true desert regions. The small ocelli of most of the males also

⁵ An inquiry adressed to Dr. Champlain was made regarding possible data regarding the host. Unfortunately no exact data on the host species involved were available.

⁶ It should also be stressed that there is good evidence that the species of the genus overwinter in the north as adults. At least the fertilized females must pass the winter, since collections made of females (at St. Clair, Ill.) in January indicate this. Whether any of the species pass the winter in the egg, larval or pupal stages is unknown.

substantiate this. Furthermore, the distribution of the group is nearly complementary to that of the Sphæropthalmine wasps, which are nocturnal, decidedly xeromorphic forms. Ephuta is nearly absent from the region from New Mexico westward, only three rare species occurring in Arizona, and a single species in California. In the east the genus occurs north to Maine and Michigan, virtually into the Canadian zone of evergreen forests; in the west it occurs north into Alberta, Canada. It has, so far, not been found on the west coast of North America, except for a single species from California.

The relatively large fauna of this genus developed in the neotropical region, together with the development of many relatively highly specialized forms in that area, indicate that *Ephuta* is to be regarded as a relatively recent invasion of most of North America. Certainly, the imperfect speciation of many of the "Artenkreise" in North America indicates that there has been time only for racial evolution or only for imperfect species development. The relatively peripheral position of the North American fauna of this genus, together with the relatively generalized form of the species, can be interpreted as illustrating the theory of the peripheral distribution of the generalized, or primitive forms of a group.

INTRAGENERIC PHYLOGENY AND CLASSIFICATION

For present purposes, the relationship of only the nearctic forms need be treated. These forms are clearly divisable into three groups on the basis of the males, as follows:

- 1. Subantennal carinæ dentate about half-way or more their distance down to the anterior clypeal margin, (Fig. 3d), thus with a subantennal basin (Fig. 2a) subequal in height to the clypeal basin (Fig. 2b); genæ never distinctly carinate behind; mandibles slender, lacking a dorsal molar surface (Fig. 10); malar space insignificant.
 - Species Group GRISEA
- Mandibles slender, normal, lacking a dorsal molar surface (Fig. 24);
 malar space short; genæ distinctly carinate behind.

Species Group PAUXILLA

2. Mandibles stout, dilated, with a broad molar surface, obliquely truncate apically (Fig. 11); malar space large, nearly twice as long as in above groups; genæ not or scarcely carinate.

Species Group EURYGNATHUS

| An analogous division of the females into groups has been |
|---|
| attempted, without success. The females can be divided into |
| species groups as follows: |
| |
| 1. Hypopygium armed with an elevated V-shaped process; pygidial area |
| setigerously punctured, defined by lateral carinules; hypostomal-sub- |
| genal carinules complete |
| (E. tumacacori) |
| 1. Hypopygium nearly flat, and without a prominent elevated V-shaped |
| process; pygidial area (if distinct) glabrous and impunctate 2 |
| 2. Pygidial area distinct, defined by lateral carinules3 |
| 3. Hypostomal-subgenal carinules complete4 |
| 4. Head densely sericeous pubescent (in addition to the sparse |
| erect vestiture); disk of second tergite with maculæ of similar |
| hairs (except E. baboquivari) E. albiceps Complex |
| (E. albiceps, auricapitis, baboquivari) |
| 4. Head lacking decumbent sericeous vestiture on vertex, with |
| sparse erect hairs only; disk of second tergite lacking maculæ. |
| 1 0 |
| E. scrupea Complex |
| (E. tentativa, E. scrupea, E. minuta) |
| 3. Hypostomal-subgenal carinules incomplete5 |
| 5. Head with a slight to distinct sericeous pubescence (in addi- |
| tion to the sparse erect vestiture); disk of second tergite |
| with maculae of similar hairs (except E. dietrichi). |
| E. grisea Complex |
| (E. argenticeps, E. coloradella, |
| E. conchate, E. floridana) |
| 5. Head nearly bare, except for sparse erect vestiture of vertex; |
| disk of second tergite lacking maculae E. puteola Complex |
| (E. puteola, E. slossonæ) |
| 2. Pygidial area vestigial or absent; hypostomal-subgenal carinules |
| complete; head densely sericeous pubescent; second tergite macu- |
| late E. sudatrix Complex |
| (E. puteola, E. margueritæ) |
| |

It will be seen that females belonging to three of these complexes (Scrupea, Grisea, Sudatrix Complexes) have males in Species group Grisea. A wholesale correlation of males and females is therefore made virtually impossible. Parallel reduction in the female sex may be a contributing factor to the difficulty in correlating the "Arten-Kreise" or "Species Groups" existing in the male and female sexes. For the present, the division based on male characters is followed, since it appears based on sounder and more reliable characters. (The Species Group Grisea will probably be found to be divisible into several discrete groups of males).

The Groups Pauxilla and Eurygnathus are endemic in the nearctic region, although the former extends southward at least into Mexico. The first group, Species Group Grisea has a much more extended distribution; it serves to connect the two other groups with the vast neotropical fauna, in most of which the clypeal type described for Species Group GRISEA exists, with various minor modifications. It is therefore believed that this type is the generalized, "primitive" type.

There are, in addition, a large number of neotropical groups, with specialized morphological features in the male sex, such as armed mesopleura, armed scutelli, armed propodea, elongate petioles, and other characteristics. These groups are only very distantly related to the nearetic species that typify *Ephuta*, as delimited by Ashmead.

All of the nearctic forms, in the male sex, may be further diagnosed as follows. This diagnosis is purely negative, and will serve to separate them from a large number of neotropical species groups:

Mesopleura never tuberculiform or spiniform produced, never divided by an oblique sulcus; petiole always short, transverse in dorsal profile; propodeum never armed laterally; subantennal carina never fused into a median carina above; gaster always rather strongly punctured; the second segment never merely punctulate; body and wings never violaceous or metallic; tergites 3 and 4 always distinctly longitudinally carinate, like the distal tergites; vestiture of gaster never exceedingly dense.

It is thus apparent that the nearctic species, excepting the two forms with modified mandibles, belong to the least specialized and derivative members of the genus.

In an ascending series, the nearctic forms can be arranged in a series as above; from the relatively unspecialized members of group GRISEA, which are annectant to the least derivative neotropical forms, on one hand, and to the nearctic group PAUXILLA on the other hand. The small, but distinctive group EURYGNATHUS, in turn, is to be derived from near group PAUXILLA.

CHARACTERS USED IN GROUP AND SPECIES DIAGNOSIS

MALES

In *Ephuta*, as in most other genera of Mutillidæ, the males retain many more differential characters than the females; hence they can express species differences in a more varied and in a greater number of ways. The taxonomy of the genus, thus, must be largely based on a consideration of the male sex. The fundamental characters of the males allow a separation into three groups of species, founded on the following characters:

The head, below and between the antennal fossæ, bears two more or less diverging clypeal carinæ that run down towards the anterior clypeal margin. These carinæ are usually more or less dentiform produced between one-fifth and three-fifths of their distance down to the clypeal margin (Fig. 3d), and often have a more or less transverse ridge or convexity connecting these two dentiform or angulate protrusions (Fig. 5e). There are, therefore, generally two basins or areas defined, one directly below the antennæ (hereafter referred to as the subantennal basin or pit (Figs. 2a, 5a), depending on its size), the other directly below that, i.e., below the transverse convexity or ridge connecting the angulations or protrusions of the subantennal ridges (this is referred to as the clypeal basin) (Figs. 2b, 5b). In the Species Groups PAUXILLA and EURYGNATHUS the subantennal pit is greatly reduced by the encroachment of the clypeal basin (Figs. 11, 24), and may be virtually absent; it is frequently not separated by a transverse ridge from the clypeal, and then is spoken of as "declivent evenly into the clypeal basin' (Figs. 11, 12). In both these groups, the subantennal carinæ are angulate or dentiform at from one-fifth to two-fifths of their distance to the anterior clypeal margin. In the third group, Species Group GRISEA, the carinæ are dentiform produced half or more their distance to the anterior clypeal margin, and the subantennal basin is therefore more or less elongate, and not pit-like (Figs. 2-4, 10). In the Species Group PAUXILLA (and to a lesser degree, in Group EURYGNA-THUS) the genæ are coarsely sculptured and separated by a distinct ridge on each side from the unsculptured, smooth, hypostomal region of the head (Fig. 37); in Group GRISEA the genal ridge is entirely lacking (faintly indicated in tegulicia Bdly.), and the genæ are evenly rounded into the posterior portions of the head. Group GRISEA always has the malar region very short (Fig. 10), and the mandibles slender and falcate, not produced into a dorsal molariform, rounded tooth. In this character Group GRISEA agrees with Group PAUXILLA (Fig. 24); the third group, Group EURYGNATHUS, however, has a larger malar distance and has large, dilated mandibles, bearing a dorsal flattened molar tooth (Fig. 11).

A number of other characters are used in diagnosing the various species in each of these main evolutionary lines. The size of the ocelli, and the form of the subantennal carinæ, with the resulting configuration of the subantennal basins and clypeal basins is (within certain limits) a valuable species character. The degree of development of the sculpture, and development or absence of a sericeous, decumbent vestiture are also important species characters. The humeral prothoracic angles may be strongly or weakly developed and bear a ventrally descending carina (Fig. 37) that bifurcates (with one branch continuing ventrad, and a second, the oblique lateral pronotal carina, cut ting the lateral pronotal faces obliquely and more or less bisecting them). The degree of development of the humeri (within certain limits) and of the oblique carina are important species characters. The form and sculpture of the tegulæ, and degree of development of the carina that traverses the base (and sometimes the whole tegula) is specific for the various species. presence of a distinct separation, or transverse ridge, cutting the propodeum into a dorsal and into a posterior face (Fig. 37) is an important species character; in some species this ridge may. be strongly produced as a median tooth; in some tropical forms the middle or sides, or both, of the propodeum may be armed with spines, tubercles, or ridges. The mesopleura of the nearctic species are uniform and offer few species characters, except as regards the density of the decumbent vestiture; in tropical forms they may be armed with a spinose process above. The scutellum

⁷ In abnormally small individuals the humeral angles are occasionally very poorly developed, compared with the normal condition for the species.

may be nearly flat, or it may be gibbous, or it may be sulcate medially, and may have each side produced into a posterior spine. The form of the petiole is uniform in our species; some tropical forms, however, have it elongate and cylindrical; the ventral carina of the petiole is sometimes constant in its degree and type of development. The sculpture of the second tergite is often of specific importance. The color of the hypopygium is nearly always of specific importance, or rather, is correlated with other characters of specific importance; in some species it may be a yellowish white, in others virtually concolorous with the pygidium and rest of the body.

Finally, the pigmentation of the integument and nature and pigmentation of the vestiture may be of specific importance, though more often only of racial importance (as in most other aculeate Hymenoptera). In some species the second segment of the abdomen may be erythrisized, in others, the whole gaster; in another form the thorax may in addition be largely ferruginous; in three species the whole body is ferruginous; a single species has only the appendages (and tegulæ) more or less completely ferruginous. With these exceptions the body and appendages of these wasps are entirely black in the nearctic forms; in no species of the nearctic fauna is there any trace of iridescence. The predominant color of the integument is then black, of the gaster as well as head and alitrunk.

This contrasts the genus with *Timulla*, and the two other neogetic genera of Mutilline, *Chætotilla* Schuster and *Physetopoda* Schuster, in which the predominant color is ferruginous or orange on the gaster (there never entirely black), and largely or entirely black on head and alitrunk. The vestiture, furthermore, differs from these three genera in being nearly uniformly pale (white or silvery), with only localized development of fuscous vestiture on the vertex, mesonotum, second and distal abdominal tergites; its degree of development, as well as absence of vestiture other than white pubescence, is specific in nature. To some degree the development of the distal sericeous band of hairs of tergite two (characteristic, on the whole, as a generic feature) is of specific importance, as well as the presence or absence of similar (less dense) vestiture on the dorsum of the propodeum and the distal abdominal tergites.⁸

FEMALES

In Ephuta the extreme reduction of the females results in a correlated "conservatism" as regards evolution of morphological species that is scarcely matched in any other Mutillid genus. The loss (in nearctic species) of the scutellar scale, and the extreme uniformity of the thoracic shape (Fig. 25), both of which afford excellent characteristics for separating species in the related genus Timulla, as well as the evolution of only two types of pigmentation and pubescence pattern (in the North American forms) result in a uniformity of form and livery that makes study of the females at once monotonous and challenging, from the taxonomic point of view. In the North American literature there is but one species of female listed, puteola Blake. Melander (1903) described a second species, as Mutilla sudatrix, which has remained unrecognized until the present. Brimley (1938, p. 438) indeed went so far as to state that puteola is "the only species of the genus known of the female sex," totally disregarding the considerable number of species of Ephuta described in the female sex from the neotropical realm.

Consideration of the rather large number of males that are known, and which differ in important morphological characteristics from each other, hence must be recognized as morphological species, leads to the conclusion that there must be more than two species of females in our region. Critical study of over 150 specimens of the female sex, at first revealed but few characteristics on which to base species, and most of these so trivial and difficultly perceptible that the description of species based on such characters would be assailable from the "practical" taxonomic point of view. On the other hand, these trivial characteristics appeared, on further study, to be constant and valid for species differentiation.

⁸ In several species where series have been examined it was found, however, that there was a decided correlation between large size and development of such vestiture, on dorsum of propodeum, apex of tergite two, and on the distal abdominal tergites, and between small size, and the lack of development of such vestiture. The density of the pubescence is therefore at least in some species correlated with size differences and is therefore not of any great importance as a species character.

Head: The size of the eyes is rather variable, and to some degree useful in distinguishing species (Figs. 38-39). In the PAUXILLA complex, preliminary work indicates it may serve to separate the female sex of the large-eyed E. battlei Bradley from the small-eyed E. pauxilla. The eye-size is to be recorded as related to the frontal distance between the eyes. The supraclypeal arched, transverse, normally quadridentate ridge, though very variable, seems to vary so much intraspecifically, that its use for species discrimination is very limited, when at all feasible. The venter of the head, bearing a pair of initially convergent, then subparallel carinæ (Figs. 40-41), or faint carinules (homologous, for at least part of their distance, with the hypostomal ridges) offers significant differences, but the degree of development of the carinules, and especially of the erect teeth near their anterior ends, is quite variable in at least some of the species. These carinæ may become obsolete before the occipital carina is attained (Fig. 40), or may end in the occipital carina (Fig. 41); with some limits these two conditions are valid for separating species. The degree of development of the occipital carina may also be specific in nature; it is so difficult to perceive that it has not been extensively used here. The antennæ are rather uniform, but there is considerable variation in the length of the first flagellar segment, as related to its width, and to the length of the pedicel and second flagellar segment; to a limited degree differences in this regard are to be considered of specific importance. Finally, the vestiture of the head (whether limited to the sparse, erect hairs issuing from the macropunctures of the frons or vertex, or whether with an additional vestiture, issuing from micropunctures, of short, sericeous, curly, silvery or golden hairs; also the density of this sericeous vestiture) is of obvious importance taxonomically. The sculpture (coarseness, depth, and density) varies widely, but must be used with caution, since small individuals always are more finely punctured than large individuals; for this reason sculpture has been avoided in the keys when possible.

Thorax: The thoracic shape is subject to variation within rather narrow limits; this variation, if sometimes specific in nature, is so intangible that it has had to be avoided as a species or descriptive characteristic. The nature of the erect vestiture, and its pigmentation, also vary so widely that specific differentiation based on them does not seem warranted. The presence of a median propodeal line of sericeous curly hairs, however, appears to be correlated with other characters of specific importance. The color of the legs varies from ferruginous to black or almost black; this variation, which may be the sum total expression of a single gene factor, could not by itself be considered as specific or varietal in value.

Abdomen: The presence of maculæ of the second tergite (Fig. 25), and whether these are large and obvious, or consist merely of a limited number of inconspicuous hairs, appears decidedly of specific value in segregating species, and is always correlated with other characteristics of specific importance. The form of the fascia of silvery sericeous hairs of the apex of tergite two also, within limits, appears taxonomically significant. The pigmentation, and livery, of segments 3-5 dorsally are, within limits, of

great value in differentiating species; in the puteola complex, unfortunately, there is little significant variation in this characteristic. The pygidial region offers characteristics of prime taxonomic significance; the pygidium may be virtually undefined (as in the sudatrix complex, Fig. 34) or may be distinctly delimited by fine ridges on the apical fourth or fifth of the ultimate tergites (Fig. 26, 31); the pygidial region may be impunctate and glabrous (Fig. 26), or (as in the tumacacori complex) may bear conspicuous appressed pubescence, arising from distinct pygidial punctures; the pygidial area, if glabrous, may be very narrow (as in minuta, Fig. 31), and less than one-fifth to one-sixth the width of the frontal interocular distance of the head, or it may be wide (and over one-fourth that width, Fig. 26); the pygidial area may be virtually polished and smooth (Fig. 26), or may be quite granulose (Fig. 31). The hypopygium also offers excellent specific characters; the sculptured hypopygial region may be slender and longer than wide at base (as in the sudatrix complex, Fig. 33), or may be as wide as long (Figs. 29, 30, 32); at its base the hoppygium usually bears a pair of glabrous, shining tubercles (near the basal, lateral corner of each side) (Figs. 29-30), which may be connected by a prominent ridge (Fig. 36); in a few species these tubercles are absent. The form of the apex of the hypopygium is also of some significance, though often nearly indeterminable; in some species the apex is truncate or nearly so, and the sides do not bear projections (Figs. 27, 32); in other cases the tip is retuse or emarginate, and the sides before the apex each bear a distinct tooth or tubercle, the apical portion of the hypopygium thus appearing quadridentate (Figs. 28-30, 36). This dentition is often very difficult to observe; in a number of individuals it could not be determined, without doubt, whether teeth were present or absent, but in most cases the character is easily observable, even from above. When the lateral teeth or tubercles are well-developed, they appear to be bent dorsad, and seem to function as guides for the pygidial plate, which they tend to keep in a position of strict opposition to the hypopygial plate. It may be possible that these teeth, in old individuals, may be nearly worn away, and misdeterminations may be made on that account; this does not invalidate the characteristic. In doubtful cases the hypopygium has to be dissected away, and can then be studied on a slide, and mounted on a small triangular point beneath the insect.

It can thus be seen that the specific characteristics of the females are few indeed, and not very satisfactory at best. Statistical study of the variation in the head capsule and thoracic shape may yet result in clearer definition of the species, especially if possible heterogonic variation is taken into account.⁹

⁹ It should also be stressed that a division of the females, on morphological grounds, into species groups is very difficult. It has been impossible to divide them into groups even approximately analogous to the three major groups recognized in the male sex (see p. 15).

KEY TO MALES

- 1. Subantennal basin subequal in height to clypeal basin (Figs. 2-4, 10), the subantennal carinæ dentiform produced or angulate about half their distance from anterior clypeal margin (or not dentiform at all); genæ evenly rounded into postgenal regions, not separated from them by genal ridges; antennal scrobes lacking distinct ridges running up them and obliquely outward (Fig. 10); mandibles slender, not dilated. Species Group GRISEA
- 1. Subantennal basin small or obsolete, pit-like if at all separated from the very large clypeal basin (Figs. 5, 7-9, 11-13, 24); the subantennal carinæ dentiform or angulate about one-fourth their distance from their dorsal origins; genæ separated by slight to distinct ridges from the postgenal regions (Fig. 37); antennal scrobes usually with indications of ridges running up and outward from them (Fig. 24)

- 6. Totally ferruginous (except for hypopygium); mesopleura very sparsely and obscurely pubescent; tergites 3-5 largely fuscous pubescent; yellow hypopygial color not extending on to pygidium.

E. floridana n. sp.

- 7. Ocelli large; interocellar distance subequal to ocellar length; ocellocular distance 1.6—1.7 the ocellar length; subantennal basin narrow, gutter-like, 3-4 times as high as wide, less than one-third the width of the clypeal basin (Fig. 18); transverse propodeal ridge strongly dentiform medially, with the dorsal face sparsely sericeous E. psephenophila n. sp.

- 9. Propodeum dorsally very densely pubescent, forming a sericeous mat obscuring the areolation; wings moderately infuscated.
 - E. margueritæ subsp. margueritæ n. sp. and subsp.
- 9. Propodeum dorsally rather sparsely sericeous pubescent, not obscuring the arcolation; wings subhyaline.
 - E. margueritæ subsp. xanthocephala n. sp. and subsp.
- ¹⁰ E. californica may be sought here, since its hypopygium is buff or yellow-buff throughout. It differs from all of the species falling in this couplet by the infuscated vestiture of the mesonotum, disk of second abdominal tergite, and of the distal abdominal segments.

10. Ocelli quite small, the ocellocular distance 3.4-3.5 the ocellar length,

- the interocellar distance 2.3-2.4 the ocellar length; dorsal propodeal face devoid of dense sericeous vestiture; dorsum of pronotum not rounded into the anterior, polished face.
 - E. ecarinata subsp. neomexicana n. sp. and subsp.
- 10. Ocelli, moderate, the ocellocular distance 1.8-2.7 the ocellar length, the interocellar distance 1.5-1.8 the ocellar length; dorsum of pronotum rounded into the anterior face, which only gradually becomes impunctate.
- 11. Dorsal propodeal face sparsely sericeous, the vestiture not obscuring the areolation; ocelli large, the ocellocular distance 1.8-2.1 the ocellar length; transverse propodeal carina obsolete, medially not at all dentiform produced. Arizona.
 - E. ecarinata subsp. pima n. sp. and subsp.
- 12. Tegulæ strongly longitudinally carinate, roof-like; humeri strongly produced, sharp and acute, but with the oblique ridges of the lateral pronotal faces low and weakly developed; hypopygium black; dorsal propodeal face densely sericeous, separated from posterior face by a weak transverse ridge that is dentiform medially.

 E. tegulicia Bdly.

- 14. Ocelli large, the length of the ocellocular distance less than 2.0 their length; eyes large, the eye-length distinctly greater than their distance apart below inner excision, their distance apart above the inner excision 1.3 the eye-length; tegulæ small, with rather strong, obscure sculpture; abdominal segments 3-7 dorsally, and hypopygium fuscous pubescent; hypopygium buff-yellow, or light fuscous

 E. argenticeps n. sp.
- 14. Ocelli small or minute, the ocellocular distance 3.1-5.0 times the ocellar length; eyes smaller, length distinctly less than distance apart

| | below excision, their distance apart above excision 1.5-1.6 the eye length; tegulæ larger, smoother; segments 3-7 and hypopygium |
|-----|--|
| | silvery pubescent; hypopygium black or nearly |
| 15 | Ocelli minute, the ocellocular distance 4.5–5.0 their length; subantenna |
| 10. | carinæ "each with a weak median tooth," the subantennal and |
| | clypeal basins not sharply separated (Fig. 22). Colorado |
| | E. grisea subsp. grisea Bdly |
| 15 | Ocelli small, the ocellocular distance 3.0-4.1 their length; subantenna |
| 10. | carinæ with a strong median tooth on each side, connected by |
| | high sharp ridge (the portions of the subantennal carina dorsad o |
| | the lateral teeth often obsolete) (Figs. 14–15). Utah and Montan |
| | eastward and northwardE. grisea subsp. fuscosericea n. subsp |
| 16 | Mandibles normal, slender, lacking a dorsal molar region, bidentat |
| 10. | distally (Fig. 24); mandibular maximum width distinctly less that |
| | height of clypeal basin; malar space obsolete. Species Grou |
| | PAUXILLA |
| 16 | Mandibles stout, dilated, with a dorsal, rounded molar tooth, thu |
| | tridentate-truncate at apex (Fig. 11); mandibular maximum widt |
| | greater than height of clypeal basin; malar space moderately long |
| | hypopygium pale yellow; genal carinæ weak. Species Grou |
| | EURYGNATHUS2 |
| 17. | Gaster orange throughout, contrasted to the entirely black head and |
| | alitrunk; hypopygium fuscous; clypeal basin separated from sub |
| | antennal pit by a transverse high carina (Fig. 9); tegulæ polished |
| | smooth, with few, scattered, coarse, punctures E. copano (Blake |
| 17. | Gaster not unicolorous ferruginous or orange (or head and alitrum |
| | also largely reddish) 1 |
| 18. | |
| | pygium pale; tegulæ with only few, scattered moderate punctures |
| | propodeum obscurely transversely divided; integument black |
| | throughout E. spinifera n. sp |
| | Posterior coxæ simple, normal, unarmed1 |
| 19. | VI 100 |
| | buff); humeri usually strongly produced (0.9 or more the head |
| | width); sculpture usually very coarse; tegulæ not coarsely pune |
| | tured throughout2 |
| 19. | Hypopygium ivory-white throughout (at most buff on distal fourth) |
| | humeri usually weakly produced; suprascrobal ridges weak; ocell |
| | small or moderate, the ocellocular distance 3.5-2.2 the ocella |
| | length, the interocellar distance 2.0-1.4 the ocellar length; tegular |
| | coarsely sculptured throughout, usually confluently so (except fo |
| | narrow lateral margins) (Fig. 37); sculpture moderate, that o |
| | second tergite of distinct, sharp, close punctures; genal caring |
| | moderate, with the submandibular, transverse prolongation weal normally; entirely black, with black legs |
| 20 | Largely or entirely ferruginous: base of antennal tubercles each with |
| | |

- 20. Totally black (at most second abdominal segment reddish or orange); suprascrobal ridges running up and out from antennal tubercles weak or moderate (Fig. 24)
- 21. Head and alitrunk totally ferruginous. Central and southern Florida peninsula E. stenognatha subsp. stenognatha n. sp. and subsp.
- 21. Head and alitrunk largely or entirely black (only the mesonotum and pronotum ferruginous throughout). Northern Florida.

E. stenognatha subsp. psephenophora n. subsp.

- 23. Petiole with dorsal and anterior faces at an obtuse angle, not separated by a sharp, erect, crenulate ridge (as in Fig. 37); mesopleura sparsely silvery sericeous; second tergite of abdomen with punctures sharp and very coarse; tegulæ weakly to moderately ridged or folded, not strongly roof-like. Florida.

E. sabaliana subsp. sabaliana n. sp. and subsp.

- 24. Second abdominal tergite with small, distant punctures, with wide polished intervals separating them; transverse ridge separating subantennal pit and clypeal basin low or vestigial; ocelli small, the ocellocular distance 2.2–2.9 the ocellar length; totally black (except for castaneous legs); distal silvery fringe of tergite two very sparse, inconspicuous; humeri moderate (width 0.77–0.83 head). Transition-Upper Austral.

E. battlei subsp. transitionalis n. subsp.

24. Second abdominal tergite with coarse, more close punctures, with narrower polished intervals; transverse ridge separating subantennal and clypeal basins high and erect; second segment fre-

| quently partly or entirely | red; distal for | ringe of tergit | e two moderate |
|----------------------------|-----------------|-----------------|----------------|
| to full; humeri strongly | produced (w | width 0.85-0.95 | head width). |
| Lower Austral-Sabalian . | | | 25 |

25. Ocelli small, length of ocellocular distance 2.5-2.6 the ocellar length; second segment ferruginous on sides; Northern Coastal Plain.

E. battlei subsp. microcellaria n. subsp.

- 26. Second segment ferruginous entirely or largely. Coastal Plain.

E. battlei subsp. battlei Bdly.

26. Second segment black pigmented like rest of gaster. Piedmont.

E. battlei subsp. confusa n. subsp.

- 27. Humeri weakly developed, the thorax at humeri 0.76-0.86 the head width; humeral prothoracic width 0.74-0.82 the tegular prothoracic width; occili smaller, the occilocular distance 3.45-2.50 the occilar length; transverse subantennal carina totally absent (Fig. 12). North and east of Texas.... E. pauxilla subsp. pauxilla Bdly.
- 27. Humeri more strongly developed, the thorax at humeri 0.86-1.02 the head width; humeral prothoracic width 0.82-0.87 the tegular prothoracic width; ocelli larger, the ocellocular distance 2.2-2.5 the ocellar length; transverse subantennal carina often weakly developed (Fig. 13). TexasE. pauxilla subsp. texanella n. subsp.
- 28. Totally ferruginous (except for appendages); propodeum weakly or moderately divided by a transverse ridge; mandible with a moderately developed molar region, not wider than the lower half of mandible; clypeal basin triangular, not depressed; malar space shorter; vertex and thoracic dorsum largely fuscous pubescent.

E. slossonæ (Fox)

KEY TO FEMALES¹¹

1. Hypopygium armed with an elevated V-shaped, biramose process sharply defined by carinæ; pygidial area setigerously punctured throughout, obscured by dense decumbent silvery vestiture, laterally

11 Since the females in most cases have not been correlated with the males, they form a separate and discrete taxonomic problem, hence are treated as a unit here. The females of the species that are known, are described together with their males, but are keyed out here. It is to be noted that it has not been possible to divide the females into complexes clearly corresponding to those set up for the males, and therefore a different set of "species complexes" are set up for them.

- defined by carinules; hypostomal-postgenal carinules connecting the hypostomal teeth with the occipital carina complete, dilated to form low lamellæ near the occipital carina; tergites 2-5 with broad, dense bands of silvery sericeous vestiture, interrupted medially by dark hairs

 E. tumacacori n. sp.
- Disk of hypopygium lacking an obvious V-shaped elevation (Figs. 27-39, 32-33); pygidial area impunctate, nitid or weakly granulose-punctate (Figs. 26, 31); postgenal carinules not dilated above, if complete (Figs. 40-41); abdominal tergite two at apex with a wide silvery sericeous interrupted band, but no such bands on subsequent tergites
- Pygidial area obsolete or undefined, evenly declivous laterally, (Fig 34), nitid (at most with an inconspicuous delicate carinule on each side on the distal 1/12 of the tergite); front and vertex conspicuously pale golden pubescent (Fig. 25); second tergite with a pair of similar (sometimes obsolete) distal maculæ (Fig. 25); hypopygium subentire to more or less tridentate at apex (Fig. 33); hypostomal-postgenal ridges complete, attaining the occipital carina on either side; disk of abdominal tergite two excessively closely, deeply, sharply punctured, the transverse intervals obsolete and the punctures subconfluent

- 3a. Head with front and vertex with fuscous to burnt-golden erect stiff, and decumbent, sericeous hairs; maculæ of tergum two of abdomen dull golden; erect hairs of terga 3-5 entirely fuscous (except for a few hairs of extreme lateral margins, which are silvery). Florida.

 E. margueritæ subsp. margueritæ n. sp. and subsp.
- 3a. Head with front and vertex with pale yellowish white to ivory colored, erect stiff, and decumbent, sericeous pubescence; maculæ of second abdominal segment whitish; erect hairs of terga 3-6 largely or entirely whitish (or partly pale golden). South Carolina to Pennsylvania......E. margueritæ subsp. xanthocephala n. sp. and subsp.
- 4. Front and vertex with short, curly, fine sericeous hairs (usually obvious

| | and rather dense), arising from punctulations interspersed among the intervals between the normal, coarser punctures; disk of second abdominal tergite usually with a pair of maculæ (as in Fig. 25) of similar hairs (these often vestigial, occasionally lacking); tergites 3-5 of abdomen, and propodeum, frequently with a longitudinal median line of silvery, decumbent, brilliant hairs; apical border of tergite two of abdomen sometimes undulate and very unequally wide |
|----|--|
| 4. | Front and vertex with only the coarse setigerous punctures, from each of which arises a suberect long hair, the intervals virtually or quite devoid of punctulations giving rise to decumbent, fine sericeous hairs; disk of tergite two usually quite lacking all trace of maculæ; propodeum and distal abdominal tergites never with a median line of silvery hairs |
| 5. | Postgenal carinules complete, extending upward unbroken from the teeth opposite the base of the mentum (Fig. 41); eyes relatively large, the interocular minimum distance of front 1.0-1.2 (1.3) the eye-length; head with a dense vestiture of golden or whitish hairs |
| 5. | Postgenal carinules extending only a short distance upward from the teeth at their lower ends, then becoming obsolete (the genæ and postgenæ thus evenly continuous, usually broadly so); eyes smaller, the interocular distance 1.32–1.60 the eye-length |
| 6. | Maculæ of disk of second abdominal tergite large, obvious (as in Fig. 25); propodeum with three narrow, obscure longitudinal lines of silvery hairs; terga 3-5 of abdomen with a similar median line of silvery hairs; eyes large, the minimal interocular frontal distance 1.0-1.2 the eye-length; basal hypopygial tubercles or transverse ridge obscure or lacking 8 |
| 6. | Maculæ of disk absent; propodeum not trilineate with pale hairs; distal |
| ٠. | terga of abdomen lacking a median line of silvery hairs; basal |
| | hypopygial tubercles connected by an obvious, glabrous transverse carinule (Fig. 36) |
| 7. | Head with a dense vestiture of sericeous, glittering yellowish or golden |
| | hairs and front and vertex E. baboquivari n. sp. |
| 7. | Head with a sparse vestiture of decumbent hairs, silvery on front and |
| | lower vertex, fuscous posteriorly on vertex, the sparse erect hairs fuscous to blackish |
| 8. | Head golden or golden-yellow pubescent; front closely contiguously punctured; hypopygium distinctly quadridentate, the distal half |
| 8. | elosely, confluently punctured |
| 9. | Hypopygial basal tubercles not connected by a sharp transverse ridge, |

the base of the hypopygium thus only obscurely bituberculate (as

in Figs. 29-30); second tergite with a pair of obsolete maculæ; tergites 3-5 entirely fuscous pubescent; New York to Illinois s. to Colorado10 9. Hypopygial basal tubercles connected by a welt-like glabrous transverse ridge (thus appearing carinate but not bituberculate) (Fig. 36) 10. Vertex and front with the erect and decumbent vestiture fuscous, obscure; disk of second tergite of abdomen with punctures close; broad apical margin of second abdominal tergite with integument concolorous with that of disk of tergite; N. Y. to Illinois and westward E. conchate Mickel. 10. Vertex and front with entirely white vestiture, rather brilliant but thin; disk of second tergite with punctures well separated; integument of broad apical margin of second tergite, beneath distal pale band, pale testaceous, not concolorous with that of disk of tergites. E. coloradella n. sp. 11. Head brilliant silvery pubescent; second tergite with similar, vestigial maculæ, with the apical sericeous band very unequally wide, strongly undulate. California E. argenticeps n. sp. 11. Head fuscous to golden pubescent; second tergite, except for the median interruption, with the distal sericeous band subequally wide, not undulate; disk of second tergite quite immaculate. Eastern 12 12. Head with decumbent microsetigerous vestiture dull, more or less fuscous or griseous-fuscous. Florida. E. floridana subsp. floridana n. sp. and subsp. 12. Head with decumbent microsetigerous vestiture yellowish-tinged, relatively brilliant. Alabama-Mississippi. E. floridana subsp. dietrichi n. sp. and subsp. 13. Pygidial area very narrow, elongate oval, distinctly granulose, dull, 1/7-1/9 the width of the front between the eyes (Fig. 31); tergites 3-5 infuscated pubescent (except for the extreme lateral margins), only the pygidial tergite silvery pubescent; genal-postgenal carinules complete, discrete (as in Fig. 41); front 1.36-1.48 the eye length; puncturation of head, alitrunk and disk of tergite two not contiguo-confluent 14 13. Pygidial area relatively broadly U-shaped, smooth and more or less nitid, $\frac{1}{3} - \frac{1}{6}$ the width of the front (Fig. 26); puncturation of head, alitrunk and disk of tergite two moderate contiguo-confluent 14. Pleura of alitrunk contiguously, coarsely punctured (the punctures much closer than on genæ); apex of second abdominal tergum with the sericeous band of decumbent hairs vestigial, except near lateral margins. Arizona.

14. Pleura medially with the very coarse punctures slightly separated

(little closer than on genæ); apex of tergum two with a distinct,

E. minuta subsp. modesta n. sp. and subsp.

- wide, dense silvery sericeous band, interrupted narrowly in the middle. TexasE. minuta subsp. minuta n. subsp.

- 17. Disk of tergum two with circular, distinctly separated punctures (longi-
- 12 I have recently been able to study the type (December, 1949), but was unable to compare it with other specimens. The head is mounted separated from the body and is partly obscured by glue: hence no accurate cephalic measurements could be made; in all other characters the type agrees perfectly with the above characteristics. This represents, almost without question, the female sex of pauxilla Bdly.

- tudinal intervals never obsolete), the punctures usually moderate in size; entire second abdominal segment bright orange-ferruginous and quite concolorous with alitrunk: never showing any trace of infuscation, even posteriorly; lateral portions of pygidial tergum largely contiguously punctured, dull
- 18. Segments 3-6 of abdomen with integument orange-ferruginous, quite concolorous with second segment and with alitrunk; head with punctures contiguous, at least on front; terga 3-4 with vestiture silvery to golden; head orange-ferruginous. Texas.

E. copano (Blake)

- 20. Eyes large: the front between the eyes only 1.17-1.21 the eye-length (as in Fig. 39); malar length 0.4-0.45 the eye-length.

E. tentativa n. sp.

PLATE I.

Figure 1. Wings of *Ephuta pauxilla*, with wing venation according to the Comstock-Needham System.

Figure 2. Subantennal carinæ of *Ephuta scrupea* Say (common, generalized type).

Figure 3. Subantennal carinæ of *Ephuta scrupea* Say (common, slightly derivative type).

Figure 4. Subantennal carinæ of *Ephuta scrupea* Say (rarer, highly derivative type).

Figure 5. Subantennal carinæ of Ephuta battlei subsp. battlei Bradley.

Figure 6. Subantennal carinæ of Ephuta tegulicia Bradley.

Figure 7. Subantennal carinæ of Ephuta stenognatha n. sp.

Figure 8. Subantennal carinæ of Ephuta stenognatha n. sp. (variant).

Figure 9. Subantennal carinæ of Ephuta copano (Blake).

Figure 10. Frontal view of head of Ephuta cephalotes n. sp.

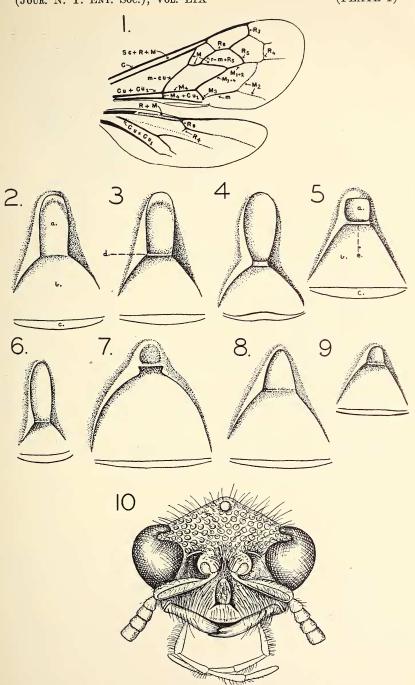


PLATE II.

Figure 11. Frontal view of head of Ephuta eurygnathus n. sp.

Figure 12. Subantennal carinæ of *Ephuta pauxilla* subsp. *pauxilla* Bradley.

Figure 13. Subantennal carinæ of Ephuta pauxilla subsp. texanella n. subsp. (extreme form).

Figure 14. Subantennal carinæ of Ephuta grisea subsp. fuscosericea n. subsp. (generalized type).

Figure 15. Subantennal carinæ of *Ephuta grisea* subsp. *fuscosericea* n. subsp. (derivative type).

Figure 16. Subantennal carinæ of Ephuta conchate Mickel n. subsp.

Figure 17. Subantennal carinæ of Ephuta margueritæ n. sp.

Figure 18. Subantennal carinæ of Ephuta ocellaria n. sp.

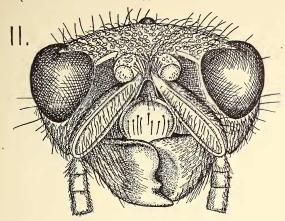
Figure 19. Subantennal carinæ of Ephuta rufisquamis André.

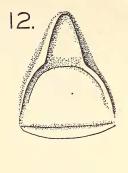
Figure 20. Subantennal carinæ of Ephuta cephalotes n. sp.

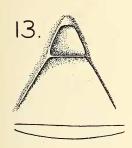
Figure 21. Subantennal carinæ of Ephuta grisea subsp. grisea Bradley.

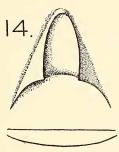
Figure 22. Subantennal carinæ of *Ephuta ecarinata* subsp. *ecarinata* n. sp. and subsp.

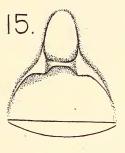
Figure 23. Subantennal carinæ of Ephuta tegulicia Bradley.

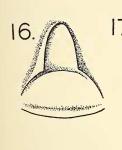


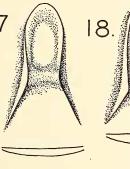


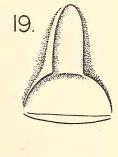


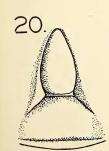




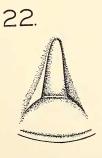












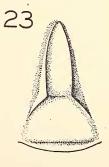


PLATE III.

Figure 24. Head (frontal view) of *Ephuta sabaliana* subsp. *sabaliana* n. sp. and subsp.

Figure 25. Dorsum of Ephuta margueritæ subsp. xanthocephala n. sp. and subsp.

Figure 26. Pygidial tergite of Ephuta puteola (Blake) (form b).

Figure 27. Ventral view of last sternite of Ephuta scrupea Say (form b).

Figure 28. Dorsal aspect of hypopygial sternite of *Ephuta scrupea* Say (form a).

Figure 29. Ventral aspect of hypopygial sternite of *Ephuta scrupea* Say (form a).

Figure 30. Ventral aspect of hypopygial sternite of *Ephuta scrupea* Say (form a).

Figure 31. Pygidial tergite of *Ephuta minuta* subsp. *modesta* n. sp. and subsp.

Figure 32. Hypopygial sternite of *Ephuta minuta* subsp. *modesta* n. sp. and subsp.

Figure 33. Hypopygial sternite of Ephuta sudatrix (Melander).

Figure 34. Pygidial tergite of Ephuta sudatrix (Melander).

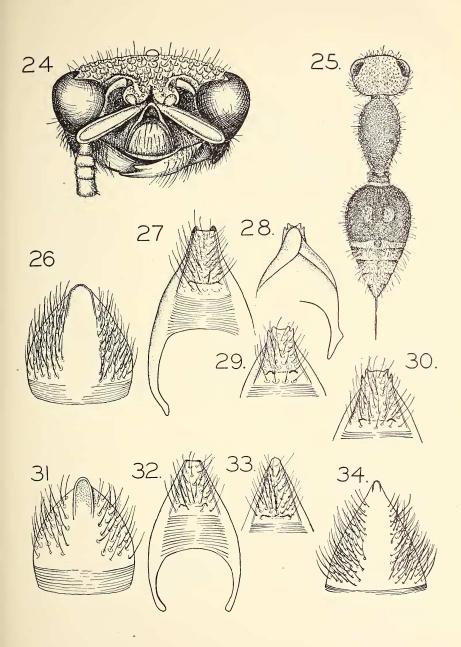


PLATE IV.

| Figure 35. | Pygidial | tergite | of | Ephuta | floridana | dietrichi | n. | sp. | and |
|------------|----------|---------|----|--------|-----------|-----------|----|-----|-----|
| subsp. | | | | | | | | | |

| Figure 36. | Hypopygial sternite | of Ephuta | floridana | dietrichi n. | sp. and |
|------------|---------------------|-----------|-----------|--------------|---------|
| subsp. | | | | | |

- Figure 37. Lateral view of male Ephuta pauxilla subsp. pauxilla Bradley.
- Figure 38. Frontal view of head of Ephuta puteola (Blake).
- Figure 39. Frontal view of head of Ephuta baboquivari n. sp.
- Figure 40. Ventral view of head of Ephuta puteola (Blake).
- Figure 41. Ventral view of head of Ephuta baboquivari n. sp.

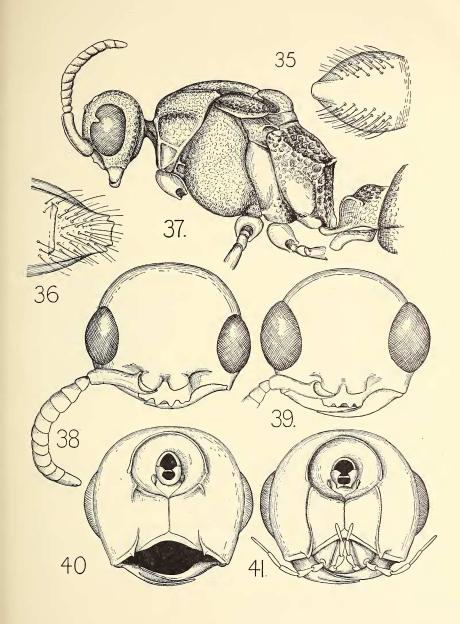


PLATE V.

DISTRIBUTION MAPS

Figure 42. Range of E. grisea

(subsp. grisea: diagonal lines; northeast to southwest).

(subsp. fuscosericea: diagonal lines; northwest to southeast).

Range of E. scrupea (males): plain crosses.

Range of E. floridana: crosses with solid centers.

Range of E. tegulicia: plain circles.

Range of E. argenticeps: four-armed circles.

Figure 43. Range of E. pauxilla (males)

(subsp. pauxilla: diagonal lines; northeast to southwest, with solid dots).

(subsp. texanella: diagonal lines; northeast to southeast, with solid center crosses).

Figure 44. Range of E. battlei

(subsp. transitionalis: horizontal lines; plain crosses).

(subsp. microcellaria: horizontal lines; solid center crosses).

(subsp. confusa: vertical lines; plain circles).

(intergrades between battlei and confusa: circles with solid centers).

(subsp. battlei: diagonal lines; northwest to southeast, with dots).

Range of E. sabaliana:

(subsp. sabaliana: plus signs).

(subsp. fattigi: quartered square).

Figure 45. Range of E. spinifera: circles.

Range of E. stenognatha

(subsp. stenognatha: solid dots).

(subsp. psephenophora: crosses).

Figure 46. Range of E. cephalotes: diagonal lines; northwest to southeast, with circles.

Range of E. margueritæ: horizontal lines; crosses.

(subsp. margueritæ: vertical lines; crosses).

(subsp. xanthocephala: solid center; crosses).

Range of E. conchate (males): diagonal lines; northeast to southwest, with dots.